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Patterns in Palaeontology: Palaeoart – fossil fantasies or recreating lost reality?

by Mark P. Witton[*1]

Introduction:

Illustrations, sculptures and animations of fossil organisms and the world around them are mainstays of palaeontology. Such restorations, known as palaeoart, are more important than they may at first seem: they help to communicate palaeontological ideas across age and language barriers; have inspired generations of scientists; and have provided the foundation of an international industry of palaeontology-themed merchandise and media worth hundreds of millions of pounds. Due to its increasing prominence and popularity, palaeoart is routinely scrutinized by scientists and the public alike. How can we infer so much about the postures, soft tissues, colours and behaviour of extinct animals when fossil skeletons — be they shells, bones or carapaces — are all that remain of them? In other words, how much of palaeoart reflects the whims and fancies of artists, and how much accurately reflects what once was?

To address this concern, we must first consider the methods employed by palaeoartists to research and execute their reconstructions. Our discussion here skims over many details for the sake of brevity, and reflects the bias of palaeoart towards fossil animals, rather than plants. However, the basic principles apply to reconstructing any extinct organism, and — hopefully — demonstrate that palaeoart is much more grounded in science than one might imagine.

Palaeoart: visualizing palaeobiological hypotheses

Palaeoart attempts to model the appearance and habits of extinct animals by blending artistry with contemporary palaeontological thinking. Wherever possible, palaeoart relies on scientific evidence rather than artistic preference. Accordingly, the line between palaeoart and palaeontological science is often blurred, to the extent that some palaeoartists — including Robert Bakker, Gregory S. Paul, Mauricio Antón and Scott Hartman — have pushed science forward through their palaeoart research. When executed well, such restorations accurately reflect how much is known about the subject species. Many artists will not restore an animal when too little data is available, on the grounds that they would have to extrapolate and speculate too much about its anatomy and appearance.

Different types of information are needed about palaeoart subjects. Studies of a single, well preserved fossil skeleton can provide the most basic information: proportions, dimensions, attainable postures and likely habits. Appreciating the broader context of that fossil — its evolutionary significance — opens up a new level of detail, however. At the heart of palaeoart beats a technique known as phylogenetic bracketing, in which the position of an organism in a phylogeny (essentially an evolutionary tree) is used to objectively infer information about its appearance and behaviour (Fig. 1). A simple evolutionary scenario demonstrates how this works. Imagine a phylogeny consisting of three species, A, B and C. Species B lies on the branch between the other two species. Species B is our subject and is poorly known, whereas species A and C are well known; they are either modern animals that have been extensively studied, or taxa with very well preserved fossils that can be described in detail. Anatomical and behavioural characteristics identified in both species A and C were probably present in their common ancestor and, by extension, any species which they 'bracket', including species B. This allows us to infer common characters of species A and C in species B even if they are not preserved. Of course, this scenario can be overturned if we discover that species B has evolved characteristics distinct from its ancestral condition, but, until then, the simplest evolutionary scenario is assumed to be the most likely.

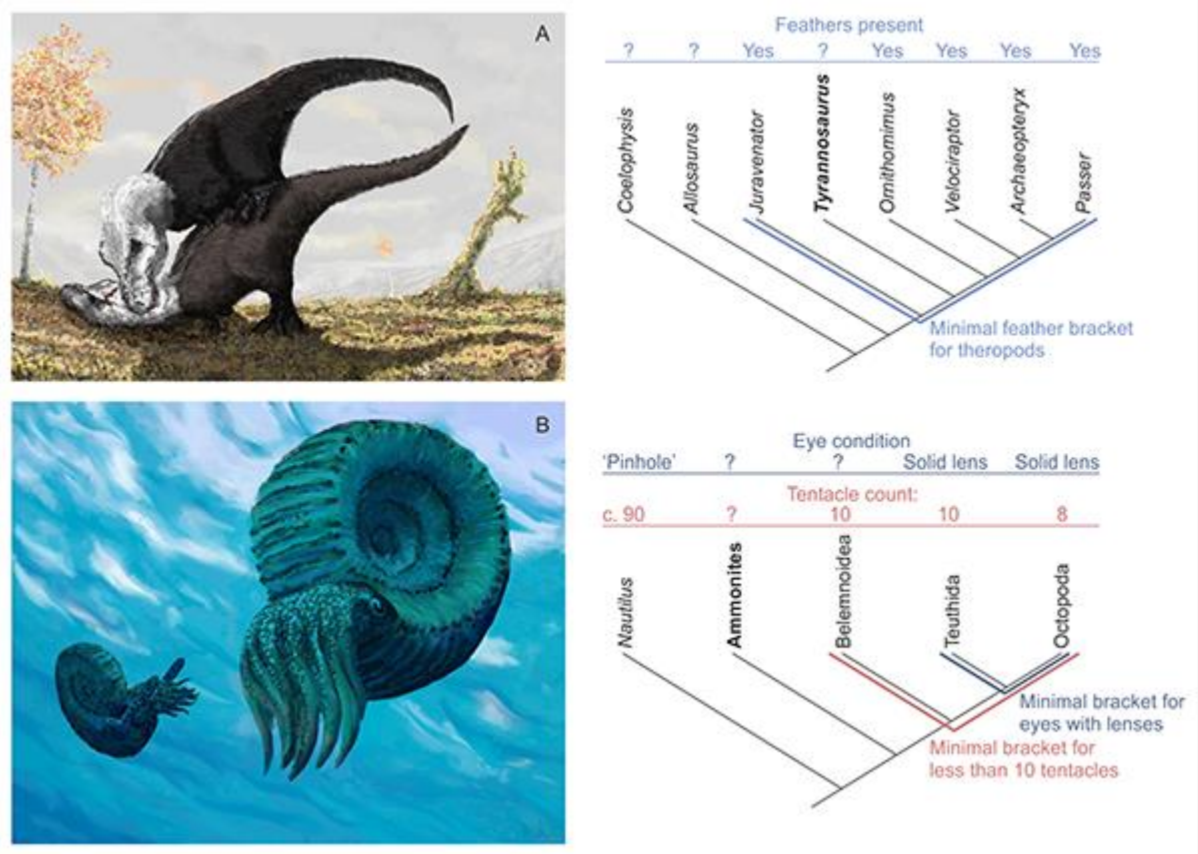

FIGURE 1 — THE UTILITY AND FRUSTRATIONS OF PHYLOGENETIC BRACKETING. A, DID TYRANNOSAURUS HAVE FEATHERS? SKIN IMPRESSIONS ARE RARE, BUT TYRANNOSAURUS BELONGS TO A BRACKET OF DINOSAURS KNOWN TO POSSESS EARLY FORMS OF FEATHERS, SO IT IS LIKELY THAT IT ALSO POSSESSED THEM (SHOWN). B, WHAT DID AMMONITES SUCH AS ERYMNOCERAS LOOK LIKE? AMMONITE SOFT TISSUES ARE VIRTUALLY UNKNOWN AND THEY OCCUPY AN POSITION OF UNCERTAIN PHYLOGENETIC SIGNAL AS GOES THEIR LIFE APPEARANCE. RECONSTRUCTIONS ARE LARGELY INFORMED BY PERSONAL PREFERENCES FOR A 'NAUTILUS-LIKE' MODEL OR A 'SQUID-LIKE' ONE (SHOWN).

The usefulness of phylogenetic bracketing to artists is obvious, allowing us to make reasoned predictions about data missing from the fossil record, including behaviour, muscle layouts, integument (skin or shell) types, and proportions of incompletely known species. Phylogenetic bracketing does not always provide definitive answers, of course, and phylogenetic scenarios with ambiguous meanings are common. For instance, if a characteristic occurs in species C, but not in species A, it is uncertain whether this was present in species B (Fig. 1B). Similarly, if the evolutionary position of a subject is not well known, or if the subject's closest known relative is actually rather distant, phylogenetic bracketing will be of limited use. When it is not possible to make reliable phylogenetic deductions, palaeoartists can apply palaeontological and biological knowledge to make reasonable suppositions about animal appearance, and hence to complete their work.

The musculoskeletal system: the foundation of a restoration

Fossils give us bare skeletons as the scaffolding from which we can hang soft tissues, but only rarely preserve the soft tissues themselves. The soft anatomy that palaeoartists are typically interested in

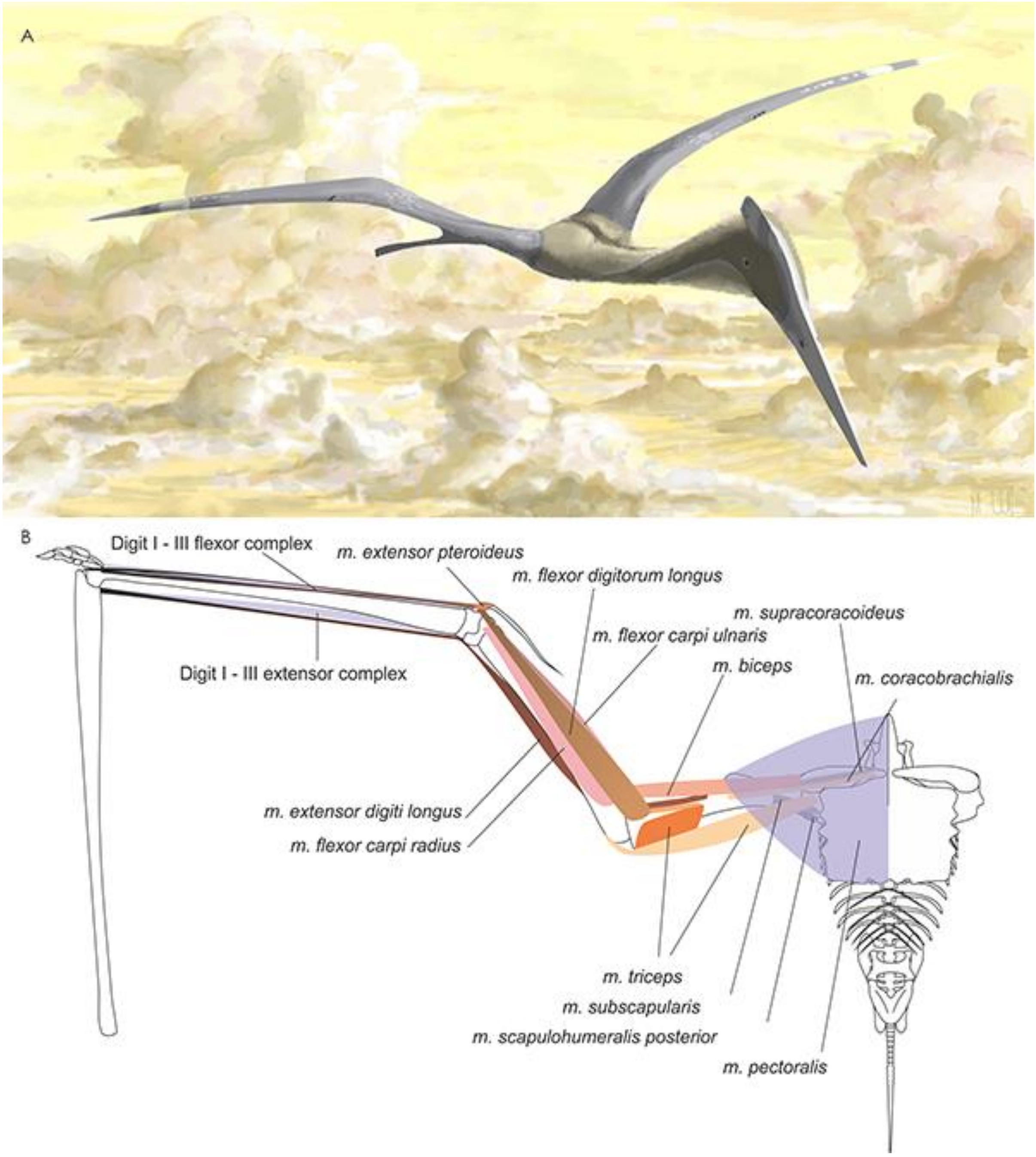

FIGURE 2 — THE WELL UNDERSTOOD RELATIONSHIP BETWEEN MUSCLE AND SKELETAL TISSUES ALLOWS US TO RECONSTRUCT THE MUSCULOSKELETAL SYSTEMS OF FOSSIL SPECIES. A, LIFE RECONSTRUCTION OF AN AZHDARCHID PTEROSAUR, WITH EXPANSIVE MUSCLES

AROUND ITS SHOULDERS DERIVED FROM B, A VENTRAL VIEW OF A PTEROSAUR TORSO AND FORELIMB SKELETON WITH RESTORED MUSCLE STRUCTURE. B MODIFIED FROM WITTON (2013).

is that which influences the external appearance of an animal — superficial musculature, fat, skin and integument, rather than deep musculature or internal organs. The musculoskeletal system of fossil species can be reconstructed with a degree of confidence thanks to phylogenetic bracketing. Muscles and tendons often leave a network of characteristic scars, tubercles and openings in skeletons, which can be correlated with those in modern animals that phylogenetically bracket palaeoart subjects (Fig. 2). These provide insights into where the muscles attach, as well as muscle identity and function, and give some idea of muscle bulk. Even complex muscular structures such as trunks and other probosces can be predicted, thanks to their distinctive muscle-attachment scarring and associated enlarged skull openings for nerves and blood vessels.

The musculoskeletal system underpins a restoration for a number of important reasons. It provides the minimal contours of the subject: whatever fats, skin or other structures we want to add, they must sit on top of these contours and, conversely, the skeleton must fit inside them (Fig. 3). The musculoskeletal system is also an important reflection of how an animal once moved, behaved and held itself, so it can strongly influence the outcome of a composition. The difference between accurate and inaccurate reconstructions of musculoskeletal systems is palpable, affecting not only the restored appearance of fossil organisms, but also our interpretations of them. Improved restoration of musculature is one of the most significant differences between palaeoart of fossil

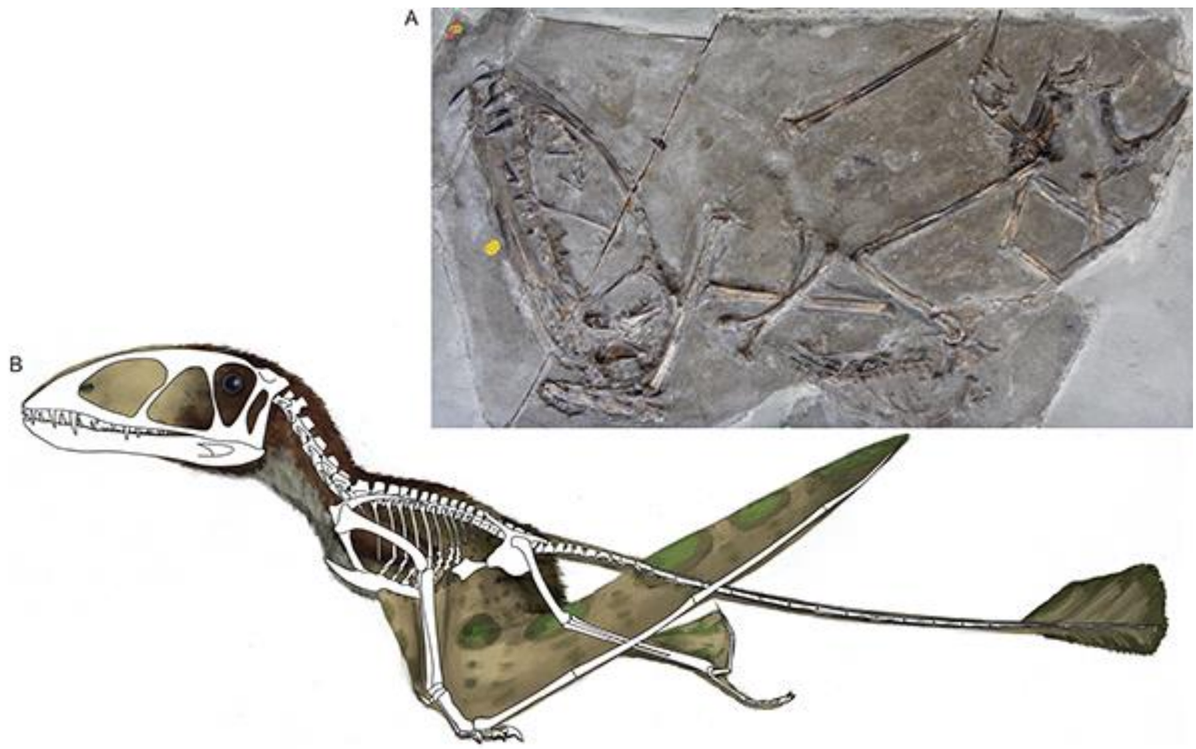

FIGURE 3 — A FUNDAMENTAL RULE OF PALAEOART: THE FOSSIL SKELETON OF AN ANIMAL MUST FIT INSIDE YOUR RECONSTRUCTION. HERE, THE SKELETON OF THE JURASSIC PTEROSAUR DIMORPHODON MACRONYX HAS BEEN RESTORED FROM NEAR-COMPLETE FOSSIL REMAINS (A), POSED INTO A LIKELY TAKE-OFF POSTURE, AND ITS SOFT TISSUES HAVE BEEN RECONSTRUCTED AROUND ITS BONES (B). MODIFIED FROM WITTON (2013).

reptiles from the 1970s onwards and that of earlier generations. Led by palaeoart greats such as Gregory Paul, Douglas Henderson and Mark Hallett, modern palaeoartists revised dinosaur from the stocky-limbed, pudgy creatures depicted in the early twentieth century to the sleeker, more bird-like animals that are now familiar to us. Alongside revisions in dinosaur science, this artwork was a major contributor to the ‘dinosaur renaissance’ of the late twentieth century.

Extraneous soft tissues

Modern animals are not merely composed of skin wrapped around their muscles and skeletons: fatty tissues, cartilaginous structures and integument also radically affect their basic appearance. However, for several decades from the 1970s onwards, palaeoartists paid little attention to this fact, producing ‘shrink-wrapped’ restorations in which every contour of the musculoskeletal system was visible, even when covered with feathers and hair. This was probably an overreaction to some of the doughier, poorly muscled creatures populating earlier palaeoart, and certainly showcased new research into muscle reconstructions; however, modern animals — even lean, physically fit individuals — do not exhibit their musculoskeletal systems quite so clearly. Modern artists are moving away from this approach by combining subtler body contours with well researched musculoskeletal systems, making for less emaciated appearances that seem — intuitively at least — more plausible.

For most healthy animals, a layer of subcutaneous fat exists between the skin and the musculoskeletal system. Unfortunately for artists, we know next to nothing about the fatty tissues of extinct species. Although it is easy enough to change the bulk of a reconstruction to simulate a well fed or malnourished individual, some modern animals concentrate their fatty tissues into bulbous masses situated in specific places — their backs, armpits or tail bases — that radically alter their body profiles. It is entirely possible that some fossil animals had similar concentrations of fatty tissues, but we have no direct evidence revealing if or where these occurred. It is sometimes proposed that the tall vertebral spines of some fossil reptiles, such as ***Spinosaurus*** (Fig. 4A), could have supported fatty humps instead of the more commonly depicted sails. This idea is not supported by the anatomy of modern species, however: no bony reinforcement is found in the fatty humps of camels, rhinos or gorillas, or in the fat, bulbous tails of lizards (Fig. 4). Bones do support some hump-like expansions of the musculoskeletal system (for example, in mammals with withers, very tall vertebral spines over the shoulders; Fig. 4F), but these are not analogous to fat stores, and reflect the need for powerful muscle systems. Several modern reptiles, including various water dragons and chameleons, have sails supported by vertebral extensions analogous to those of some fossil reptiles, and this seems a more likely interpretation of these structures (Fig. 4E). The message here seems to be that we can predict humps of muscle and sails from bones, but that we generally have very little idea how accurate our portrayals of animal fat distribution are.

Cartilage and dense connective tissues are additional problems for palaeoartists. These rarely preserved tissues support the ear flaps and noses of mammals, as well as some fins of swimming reptiles and mammals. They are therefore undoubtedly important to the appearance of certain animals. The existence and position of cartilage structures is sometimes recorded in skeletal characteristics, although bones rarely tell us much about the shape or size of these structures, and many cartilage features leave no traces whatsoever on animal bones. The same is true of skin membranes and webbing, organs that stretch between animal limbs and digits to aid swimming or flight. Our knowledge of these tissues is mostly reliant on the exceptional preservation of fossils with

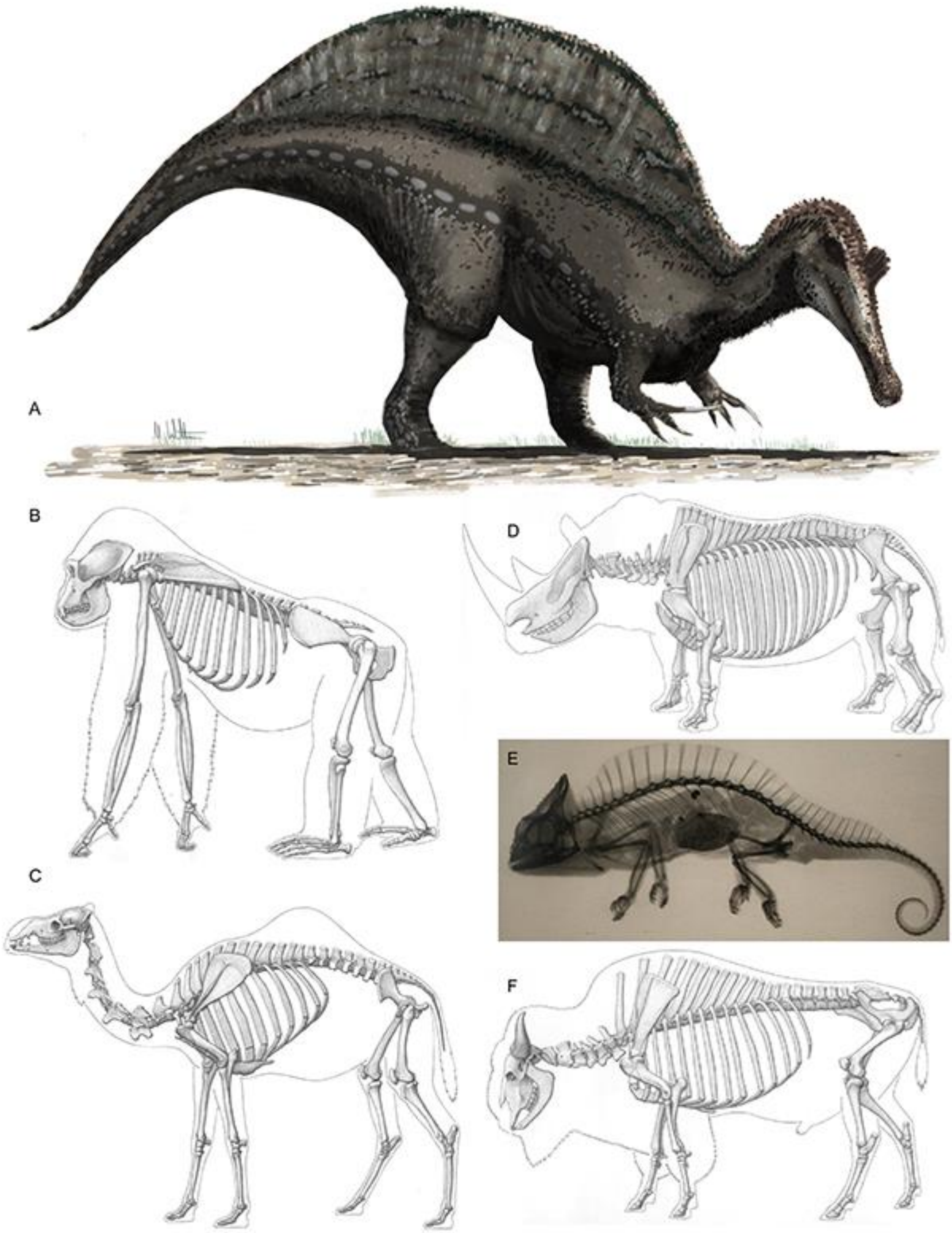

FIGURE 4 — PALAEOARTISTS RESTORE ANIMAL FATS WITH DIFFICULTY. IT HAS BEEN PROPOSED THAT LARGE VERTEBRAL SPINES IN FOSSIL SPECIES SUCH AS SPINOSAURUS AEGYPTICUS (A) SUPPORTED HUMPS OF FATTY TISSUES LIKE THOSE OF MODERN CAMELS, BUT FATTY HUMPS ARE NOT DIRECTLY SUPPORTED BY SKELETONS IN MODERN SPECIES INCLUDING (B) LOWLAND GORILLAS (GORILLA GORILLA), (C) DROMEDARIES (CAMELUS DROMEDARIES) AND (D) WHITE RHINOCEROS (CERATOTHERIUM SIMUM). VERTEBRAL SPINES ANCHOR SAILS IN SOME MODERN LIZARDS, SUCH AS CRESTED CHAMELEONS (TRIOCEROS CRISTATUS; E), AND WITHERS ANCHOR

POWERFUL NECK MUSCLES AS IN AMERICAN BISON (BISON BISON; F). B–D AND F FROM GOLDFINGER (2004); E HISTORIC X-RAY (1896) BY JOSEF MARIA EDER.

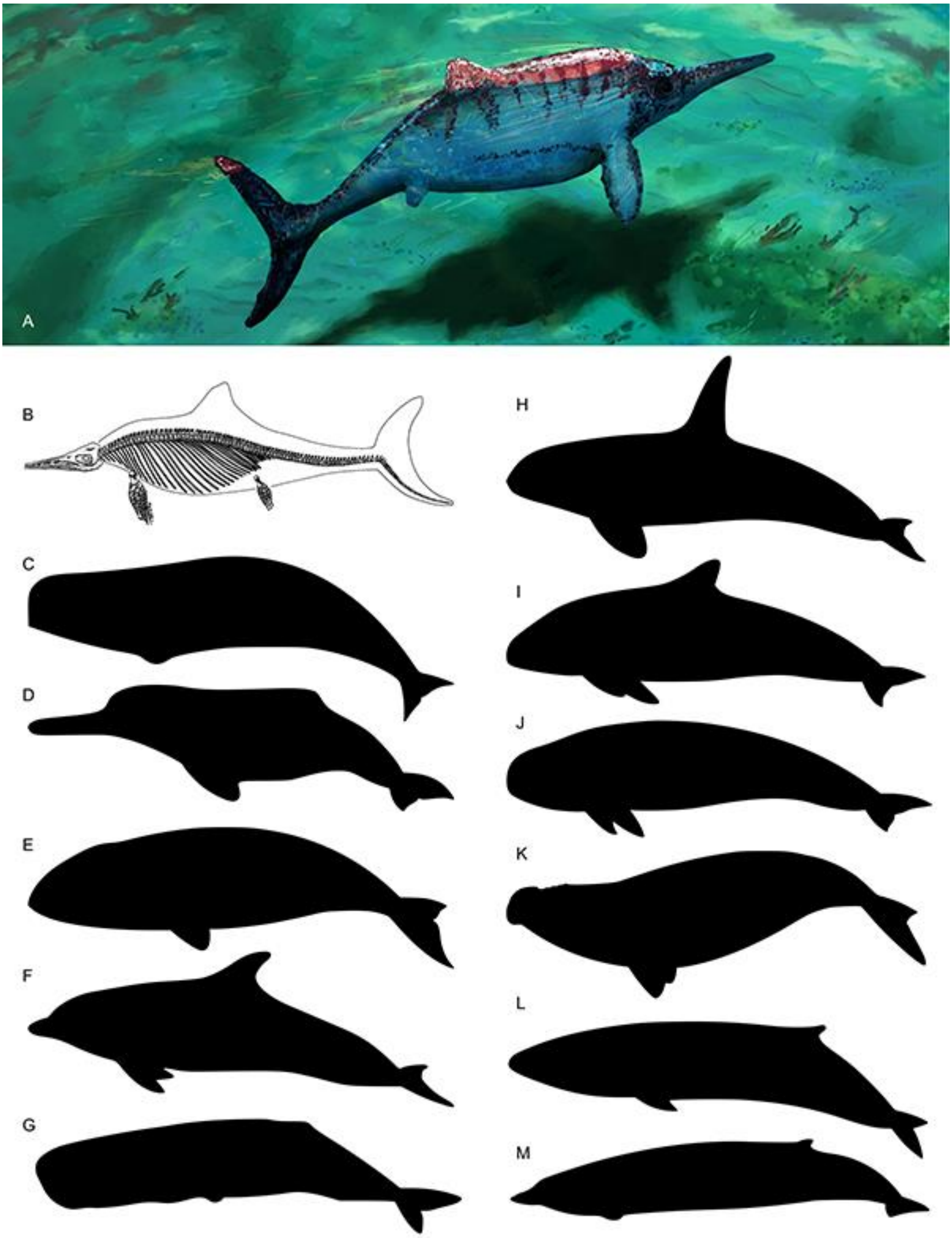

FIGURE 5 — THE DOLPHIN-LIKE APPEARANCE OF ICHTHYOSAURS SUCH AS OPHTHALMOSAURUS ICENICUS (A) IS INFORMED BY SOFT-TISSUE OUTLINES ASSOCIATED WITH A HANDFUL OF TAXA, SUCH AS STENOPTERYGIUS MACROPHASMA (B, OUTLINE SHOWS EXTENT OF SOFT TISSUE). BUT IT MAY BE UNREALISTIC TO BASE SOFT-TISSUE RESTORATION ON JUST A FEW SPECIES; MODERN CETACEANS (C–M), FOR EXAMPLE, SHOW CONSIDERABLE VARIATION IN DORSAL-FIN SIZE AND POSITION, AS WELL AS FATTY-TISSUE DISTRIBUTION. C,

BELUGA (DELPHINAPTERUS LEUCAS); D, GANGES RIVER DOLPHIN (PLATANISTA GANGETICA); E, BOWHEAD WHALE (BALAENA MYSTICETUS); F, BOTTLENOSE DOLPHIN (TURSIOPS TRUNCATES); G, SPERM WHALE (PHYSETER MACROCEPHALUS); H, ORCA (ORCINUS ORCA); I, VAQUITA (PHOCOENA SINUS); J, FINLESS PORPOISE (NEOPHOCAENA PHOCAENOIDES); K, ATLANTIC NORTHERN RIGHT WHALE (EUBALAENA GLACIALIS); L, PYGMY RIGHT WHALE (CAPEREA MARGINATA); M, BAIRD'S BEAKED WHALE (BERARDIUS BAIRDII). B MODIFIED FROM MCGOWAN AND MONTANI (2003). C–M, MODIFIED FROM DRAWINGS BY CHRIS HUH, USED UNDER CREATIVE COMMONS ATTRIBUTION-SHARE ALIKE 3.0 UNPORTED LICENCE.

extensive soft tissues. Many soft-tissue structures familiar in palaeoart — the dorsal fins of ichthyosaurs, the wing membranes of pterosaurs and the skin ornaments of some dinosaurs — are derived from just such fossils. Frustratingly, structures like these are typically represented by, at best, mere handfuls of species, so their natural variation and evolutionary history are typically unclear. Given how diverse major soft-tissue structures are in modern animals, it is highly likely that palaeoartists are under-representing soft-tissue diversity in extinct creatures (Fig. 5).

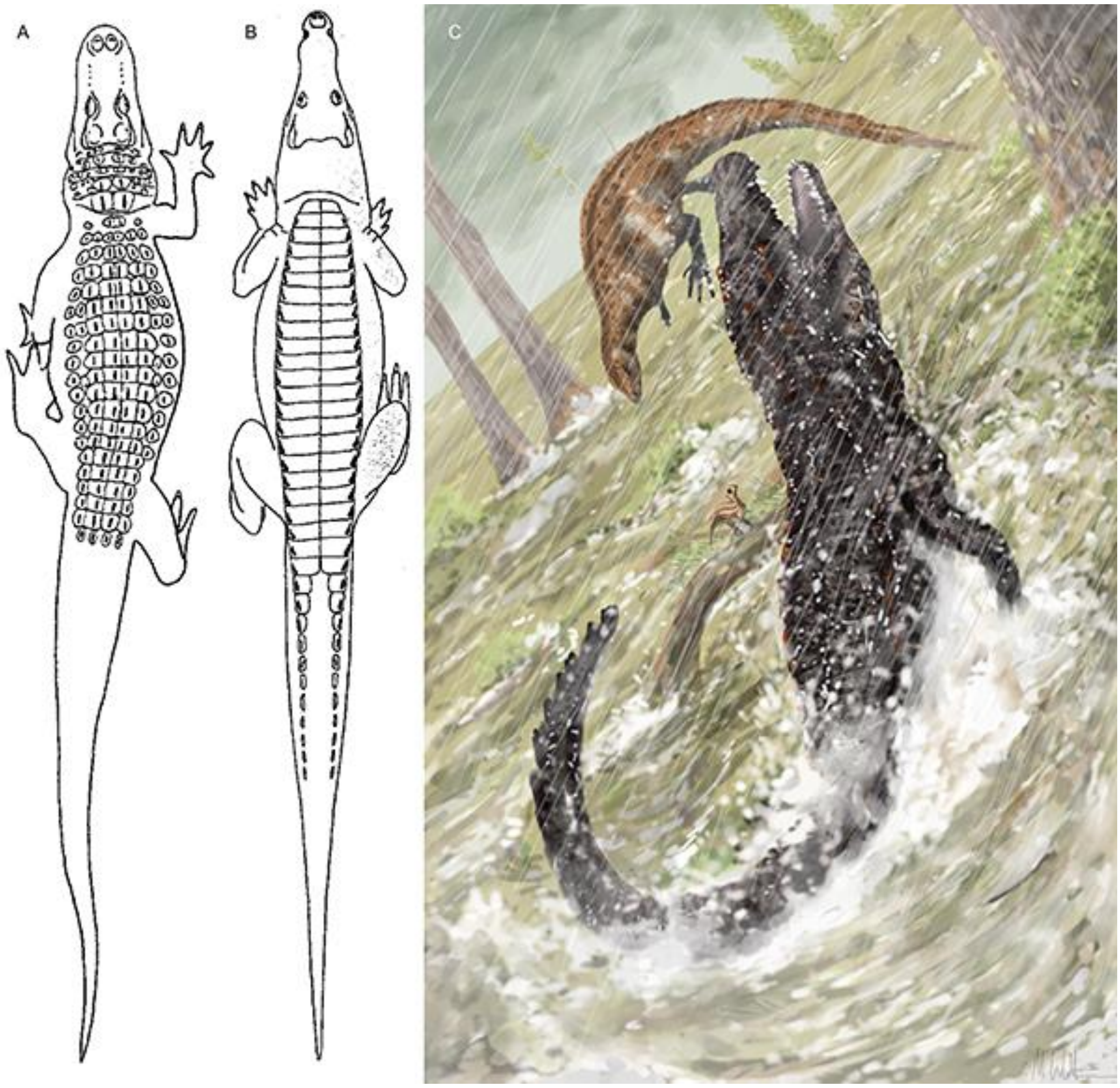

FIGURE 6 — MODERN CROCODYLIANS, SUCH AS ALLIGATOR MISSISSIPPIENSIS (A), SHOW HOW OSTEODERMS ARE OVERLAIN BY SINGLE SCALES. MANY FOSSIL CROCODYLIFORMES, SUCH AS GONIOPHOLIS SP. (B), POSSESS TWO ROWS OF LARGE, RECTANGULAR OSTEODERMS INSTEAD OF MANY ROUNDED ONES; THE BACKS OF ANIMALS SUCH AS ANTEOPHTHALMOSUCHUS HOOLEYI (C) WOULD THUS APPEAR LESS SCULPTED THAN THOSE OF MODERN CROCODILES. A AND B FROM SALISBURY AND FREY (2000).

Soft-tissue preservation is also important in integument restoration. Animal skins are rarely naked, instead being covered with scales, feathers or fur, along with claw sheaths or nails, horny beaks and other extraneous structures. Dense filamentous coverings or thick integuments can drastically alter the shapes of animals, so this is another element that palaeoartists strive to reconstruct accurately. There are several ways to predict the integuments of extinct animals. The first concerns the interactions between integument and bone. Osteoderms, bony plates that grow within animal skin to form armour, are almost always precisely overlain by single scales. These 'skin bones' allow us to reconstruct scale shapes of ancient animals, and when they are preserved in articulated sheets, entire flanks of animals can be reproduced with confidence (Fig. 6). Elsewhere, skin that lies very tight against the bone — such as in animal skulls — leaves characteristic signatures specific to scales, horn sheaths or dense skin pads. The faces of horned dinosaurs have been reconstructed in detail using these signatures. Large, shafted dinosaur feathers can also leave distinctive tubercles where they anchor to the skeleton. These are typically found on dinosaur forearm bones, and you may be familiar with them from eating chicken wings!

FIGURE 7 — IN THE PAST FEW DECADES, NEW FOSSILS HAVE SHOWN THAT MANY SPECIES OF NON-AVIAN DINOSAURS AND PTEROSAURS WERE COVERED IN FILAMENTOUS STRUCTURES ('FUZZ') ALONG WITH SCALES. DEPICTING 'MOSAIC INTEGUMENTS' OF SCALES AND FILAMENTS, AS SHOWN HERE ON THE TRIASSIC DINOSAUR RELATIVE SCLEROMOCHLUS TAYLORI, MAY BE A GOOD BASE ASSUMPTION.

More often than not, however, palaeoartists rely on integument directly entering the fossil record. Some fossils preserve carbonized integuments of entire animals, and fossil 'mummies' can preserve swathes of skin and integument draped over ancient carcasses. The detail of these fossils cannot be understated: feather counts, distribution and morphology, scale shapes and sizes, and fur length and density can be gleaned from these exceptional specimens. Unfortunately, such wonderful integument remains are not common. Most body fossils lack any trace of skin, and those that do have skin typically offer mere scraps. These provide some insight into ancient animal coverings, but modern species and completely sampled fossil integuments show the folly of assuming that small scraps of skin represent a complete picture. 'Mosaics' of integument seem to be common in some groups: mammals frequently mix naked skin and dense fur (sometimes with scales), whereas dinosaurs and pterosaurs blend scales with filamentous structures (including feathers in dinosaurs), and sometimes with naked skin. For nearly all fossil animals, therefore, it is exceedingly difficult to reconstruct integuments with confidence. The best palaeoartists can do is to depict integuments that are known to occur within the phylogenetic bracket of their subject and that seem reasonable for the anatomy, physiology and habitat of the animal concerned. This at least ensures that the basic integument types are likely to be accurate, even if the details are lost to time (Fig. 7).

'How do you know what colour it was?'

The colouration of extinct animals is probably commented on more than any other aspect of palaeoart, so it might be surprising to know that palaeoartists give this relatively little consideration. In almost all cases, extinct-animal colour is so difficult to predict that there is little point worrying about getting it absolutely right. Palaeoartists do what they can, taking inspiration from modern

FIGURE 8 — HOW DO WE KNOW WHAT COLOUR EXTINCT ANIMALS WERE? MOSTLY, WE HAVE LITTLE IDEA, BUT THIS 120-MILLION-YEAR-OLD FOSSIL MUD SNAIL (*VIVIPARUS CARINIFERUS*) IS PART OF AN EXTANT GENUS IN WHICH CREAM AND BROWN SHELL STRIPES ARE COMMON, SO IT MIGHT HAVE HAD SIMILAR PATTERNS.

animals, being mindful of phylogenetic bracketing (taking into account when certain types of skin pigmentation evolved, and if the subject animals could see in colour) and making efforts to match suitable colouration with lifestyles (no hot-pink ambush predators, please). However, colour patterns largely reflect guesswork, personal preferences and compositional considerations.

Colouration can be predicted for a minority of extinct animals. Some modern animal lineages have very close relatives in the distant past, and it is not unreasonable to assume that they have similar colours and patterning (Fig. 8). Amazingly, colour pigments can fossilize, particularly on tough tissues like feathers, cornified skin and insect cuticles. These have often lost the colour they had in life by the time of discovery, but they do at least reveal details of patterning and shading. In the past few years, research has suggested that some fossil pigment cells, known as melanosomes, tell us a great deal about extinct-animal colour. Melanosome arrangement and density can determine colour shades in modern animals, so comparing arrangements of these with fossil melanosomes provides a means of deducing colour in ancient species. This technique has been applied to a variety of feathered dinosaurs, a giant penguin, mosasaurs, ichthyosaurs and ancient turtles. Some artists have been quick to take this colour data on board, not only producing new art in line with these predictions, but also revising older work to match them.

What fossil melanosomes actually tell us about colour is debatable, however, and the technique is, at best, considered controversial. The application of high temperatures and pressures to modern feathers suggests that melanosome distributions are altered during fossilization, so preserved melanosome arrangements may not accurately reflect their condition in life. Some scientists are not convinced that fossil melanosomes can be adequately distinguished from fossilized bacterial cells: we may be interpreting microbial colonies rather than pigment information. Moreover, at least for feathers, melanosomes are not the only things that produce colour — light interacting with feather microstructure is also involved. Thus, even if the other caveats are swept aside, feather melanosomes alone still do not tell us the full story about the colouration of extinct dinosaurs. Further research may find ways to resolve these issues, but, at present, the reliability of melanosome-structure colour determination is uncertain.

And then we're done, right?

A basic reconstruction of a fossil species could be said to be complete once the creature's posture, proportions, musculoskeletal system, body fats, integument and colour have been rendered. However, one recent publication argues that palaeoart that stops at this point might be selling ancient animals short. The critically acclaimed ***All Yesterdays***, widely considered one of the most thought-provoking books on modern palaeoart (see 'Further reading'), argues that most palaeoart restorations are too conservative when compared to modern animals. Our modern fauna demonstrates much anatomy that would be undetectable in the fossil record, so ***All Yesterdays*** argues for the use of reasoned speculation in palaeoart, giving reconstructions features such as shaggy coats of filaments, thick layers of fat or soft-tissue adaptations for specialized lifestyles (Fig. 9). As long as the speculation fits the correct evolutionary context and obeys laws of anatomy, ***All Yesterdays*** argues that it is fair game. This perspective may seem jarring and at odds with the otherwise science-led approach of palaeoart, but there is something to be said for this viewpoint. Conservative reconstructions are probably as inaccurate as the more elaborate, speculative restorations, but the latter at least acknowledge the diversity of soft-tissue anatomy and adaptations of real animals. The line between reasonable speculation and outlandish fancy is undoubtedly a fine one, but scientists and laypeople alike have noted that carefully applied, well executed speculation can add tremendous plausibility and character to a reconstruction, and convey a sense that the subject species actually belong to a particular habitat.

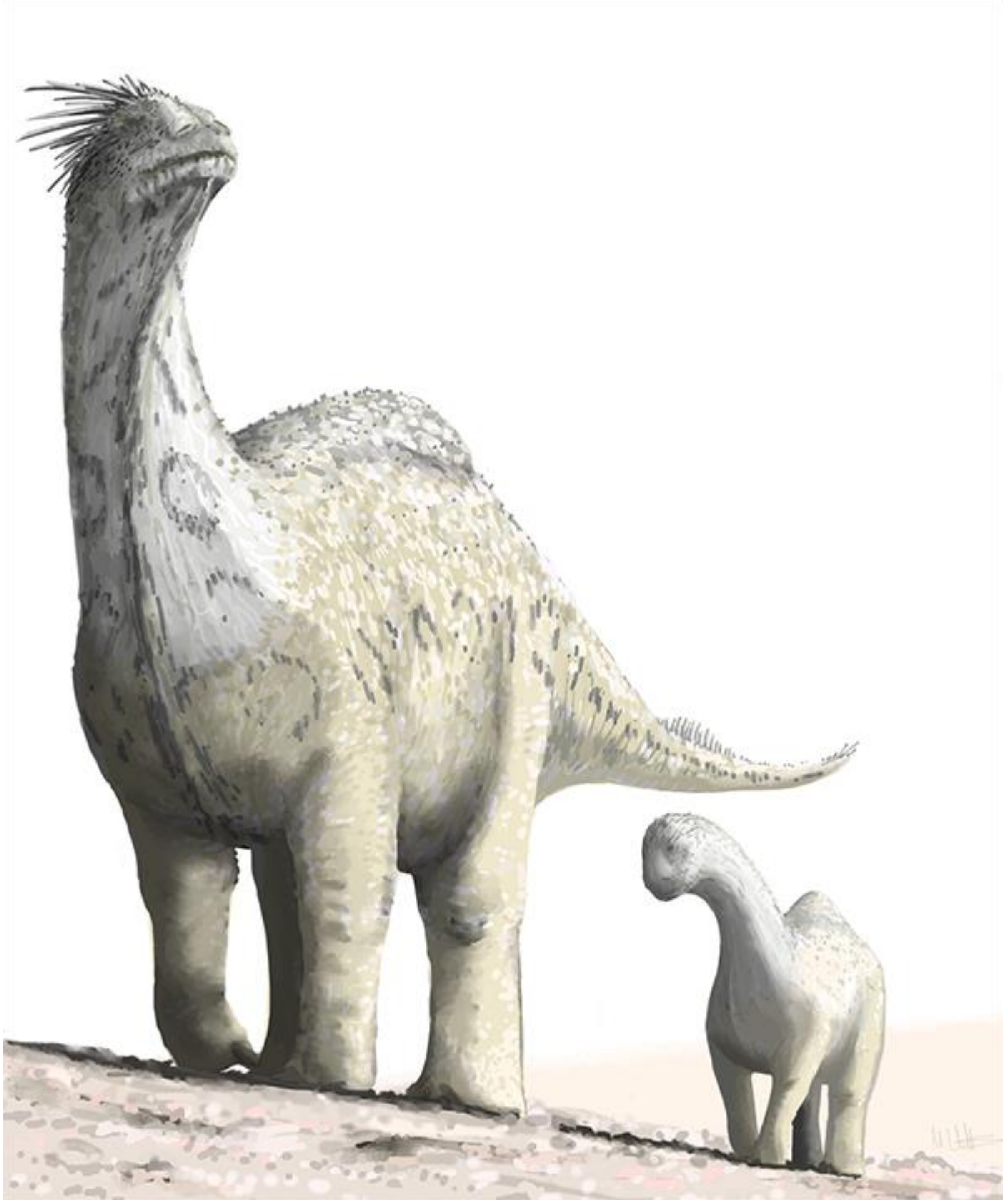

FIGURE 9 — REASONED SPECULATION IN PALAEOART. THE SAUROPOD CAMARASAURUS SUPREMUS DEPICTED WITH ADAPTATIONS FOR LIVING IN A VERY DRY ENVIRONMENT: ENLARGED NASAL CAVITIES TO AID RESORPTION OF MOISTURE, SEALABLE NOSTRILS TO REDUCE EVAPORATION, WRINKLED SKIN TO ENHANCE HEAT DISSIPATION, WHITE AND TAN COLOURING TO RESIST HEAT SOAKING, AND A FAT HUMP TO STORE ENERGY. SUCH FEATURES ARE SPECULATIVE, BUT DO NOT CONTRADICT ANY DATA WE HAVE FOR THIS TAXON, AND ARE CONSISTENT WITH THE ADAPTATIONS OF MODERN DESERT-DWELLERS.

Palaeoart: less snapshots of the past, more reflections of the present

In closing, we can now see that the answer to our original question — how much palaeoart is invented by the artist, and how much is true to (extinct) life? — is complex, depending on both the subject species and the anatomical component being scrutinized. Overall, most scientists and artists agree that the poses and musculoskeletal systems depicted in palaeoart are fairly accurate, but so many unknowns surround other aspects of animal appearance that close resemblance to ancient truths is unlikely. Few artists lose sleep over this, however, because we can never truly test how accurate our recreations are. Instead, palaeoartists aim to produce plausible 'models'of extinct life using contemporary scientific data, in much the same way that palaeontologists make predictions using evidence-led hypothesis building. This means that palaeoart should not be judged by adherence to an unknown reality, but by how it represents contemporary science (as well as, of course, artistic merit). Palaeoartworks demonstrating poor understanding of modern palaeontology can be classified as objectively inaccurate, and conversely, good palaeoart reflects detailed investigation into fossil-animal appearance. Palaeoartistry requires a unique range of skills — understanding of zoology, anatomy, botany, palaeontology and artistry — and there is a need for wider appreciation of this by scientific, educational and media institutions (Fig. 10). Ultimately, although palaeoartists cannot empirically tell us 'this is what was', they at least show ***something like*** what once existed. Given the academic, educational and financial value of this service, settling for near-truths in palaeoartistry is considerably better than the alternative.

FIGURE 10 — PALAEOARTISTS AND THEIR WORK ARE FREQUENTLY UNDERVALUED BY SCIENTIFIC AND MEDIA INSTITUTIONS. THE MODERN PALAEOART INDUSTRY IS IMPOVERISHED, RIFE WITH BORDERLINE PLAGIARISM AND DISRESPECTFUL TO THE SKILL AND EXPERTISE OF ITS PRACTITIONERS. THIS HAS TO CHANGE. A FULL DISCUSSION OF THIS PROBLEM IS DUE FOR PUBLICATION SOON, BUT DETAILS OF THE SORRY STATE OF PALAEOART ARE EASILY FOUND ONLINE. THOSE INTERESTED IN SUPPORTING PALAEOARTISTRY ARE

URGED TO RAISE AWARENESS OF PROBLEMS WITHIN THE INDUSTRY TO HELP IMPROVE DECISION-MAKING WITH PALAEOART-RELATED MEDIA.

Suggestions for Further Reading:

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